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The Future of the Shortgrass Steppe

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Where lies the future of the shortgrass steppe? In prior chapters we have described the remarkable resilience of the shortgrass steppe ecosystem and its organisms to past drought and grazing, and their sensitivity to other types of change. Emerging from this analysis is the idea of vulnerability to two main forces: future changes in precipitation or water availability, and direct human impacts.

What are the likely changes in the shortgrass steppe during the next several decades? Which of the changes are most likely to affect major responses in the plants, animals, and ecosystem services of the shortgrass steppe? In this chapter we evaluate the current status of the shortgrass steppe and its potential responses to three sets of factors that will be driving forces for the future of the steppe: land-use change, atmospheric change, and changes in diseases.

Land-Use Change and Conservation

Conservation and Management Challenges in the Shortgrass Steppe: Traditional and Emerging Land-Use Practices

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Referring to the early 1900s, James Michener in his novel *Centennial* (1974) wrote the following:

> The old two-part system that had prevailed at the end of the nineteenth century—rancher and irrigator—was now a tripartite cooperation: the rancher used the rougher upland prairie; the irrigation farmer kept to the bottom lands; and the drylands gambler plowed the sweeping field in between, losing his seed money one year, reaping a fortune the next, depending on the rain. It was an imaginative system, requiring three different types of man, three different attitudes toward life.... (p. 1081)

Even today, because of the strong water limitation for cropping, the shortgrass steppe remains relatively intact, or at least unplowed, in contrast to other grassland ecosystems (Samson and Knopf, 1994). More than half of the shortgrass steppe remains in untilled, landscape-scale tracts, compared with only 9% of tallgrass prairie and 39% of mixed-grass prairie (The Nature Conservancy, 2003). These large tracts, including those in the national grasslands (Pawnee, Cimarron, Comanche, and Kiowa/Rita Blanca), provide the greatest opportunity for preserving key ecological processes and biological diversity.

The landscape of the 1900s has been rapidly changing during the past several decades. Increased habitat loss and fragmentation threaten biological diversity in the shortgrass steppe. Land-use changes in the shortgrass steppe are similar to those throughout the United States, where, during the latter half of the 20th century, most human population growth in lower density regions surrounds urban centers, contributing to land-use shifts from agricultural to exurban developments (Brown et al., 2005; Theobald, 2005). During recent years, exurban land development increased at a rate 25 times higher than overall U.S. population growth (Theobald, 2005). During the next decade and a half, it is estimated that exurban developments will expand to 14.3% of U.S. land area. The result for eastern Colorado may be a loss from production of as much as 35% of row–crop agriculture (Parton et al., 2003). Concomitantly, the composition of the rural population is changing, as the proportion of elderly people on agricultural lands increases (Hauteniemi and Gutmann, 2005; Parton et al., 2007a).

These changes are highly significant to agricultural ecosystem services (Millennium Ecosystem Assessment Series, 2003), including food, timber, and fiber production, as well as to cultural ecosystem services associated with open space, the social structure of rural communities, ecosystem processes including productivity, and biological diversity (Theobald, 2004). The interactions among land use, social processes and cultural values, and ecosystem services represent new frontiers in both ecological and social sciences (Gunderson et al., 2005), and pose many of the most important challenges for the future of the shortgrass steppe.

In the eastern plains of Colorado, population has grown exponentially during the past 50 years (2.47% increase per year; data from U.S. Census Bureau [2000]), especially in the 11 highly developed counties bordering the Front Range of the Rocky Mountains (Fig. 19.1). Between 1987 and 2002, the number of housing units in these counties increased by 30%, to more than 1.5 million, compared with only a 2% increase in the more rural counties of the plains (data from

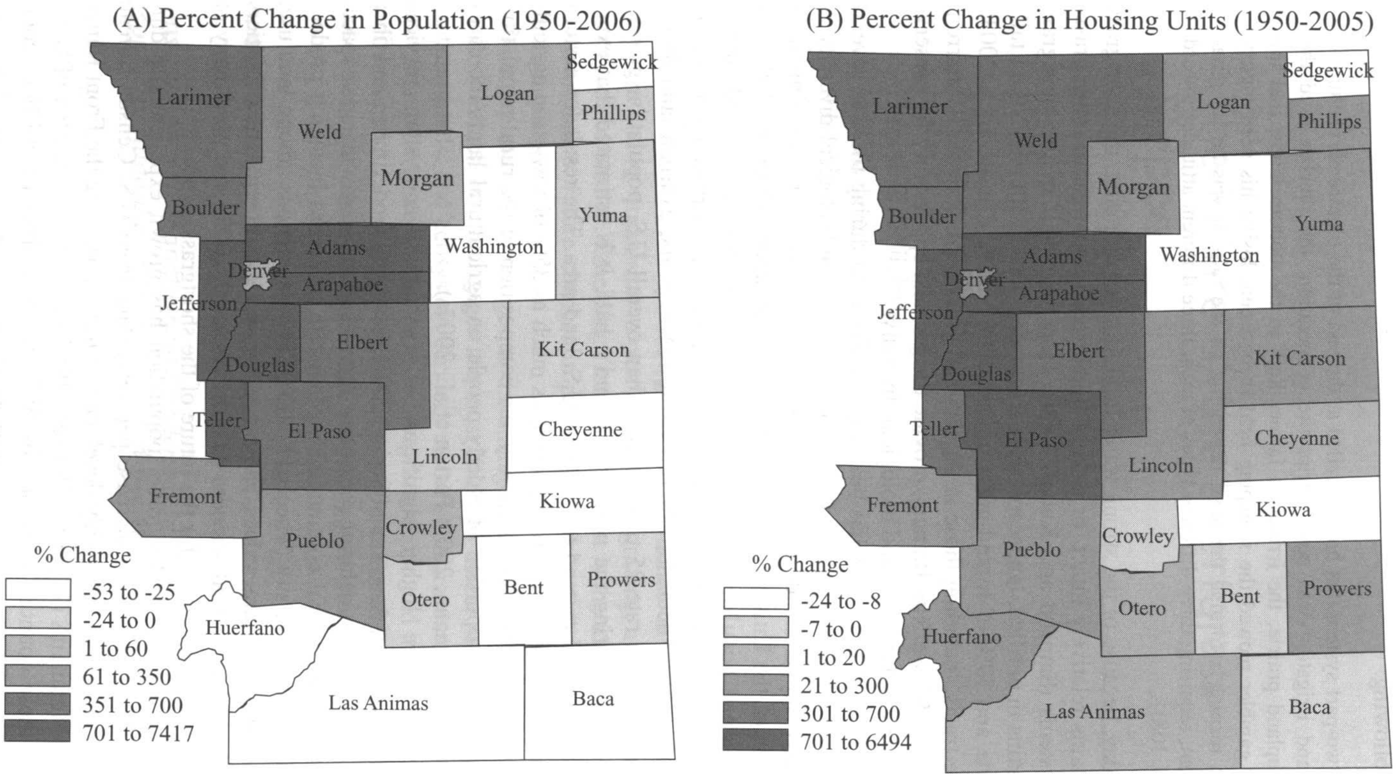

Figure 19.1 The changes in population (A), housing units (B), since 1950 for the available census data for eastern Colorado (U.S. Census).

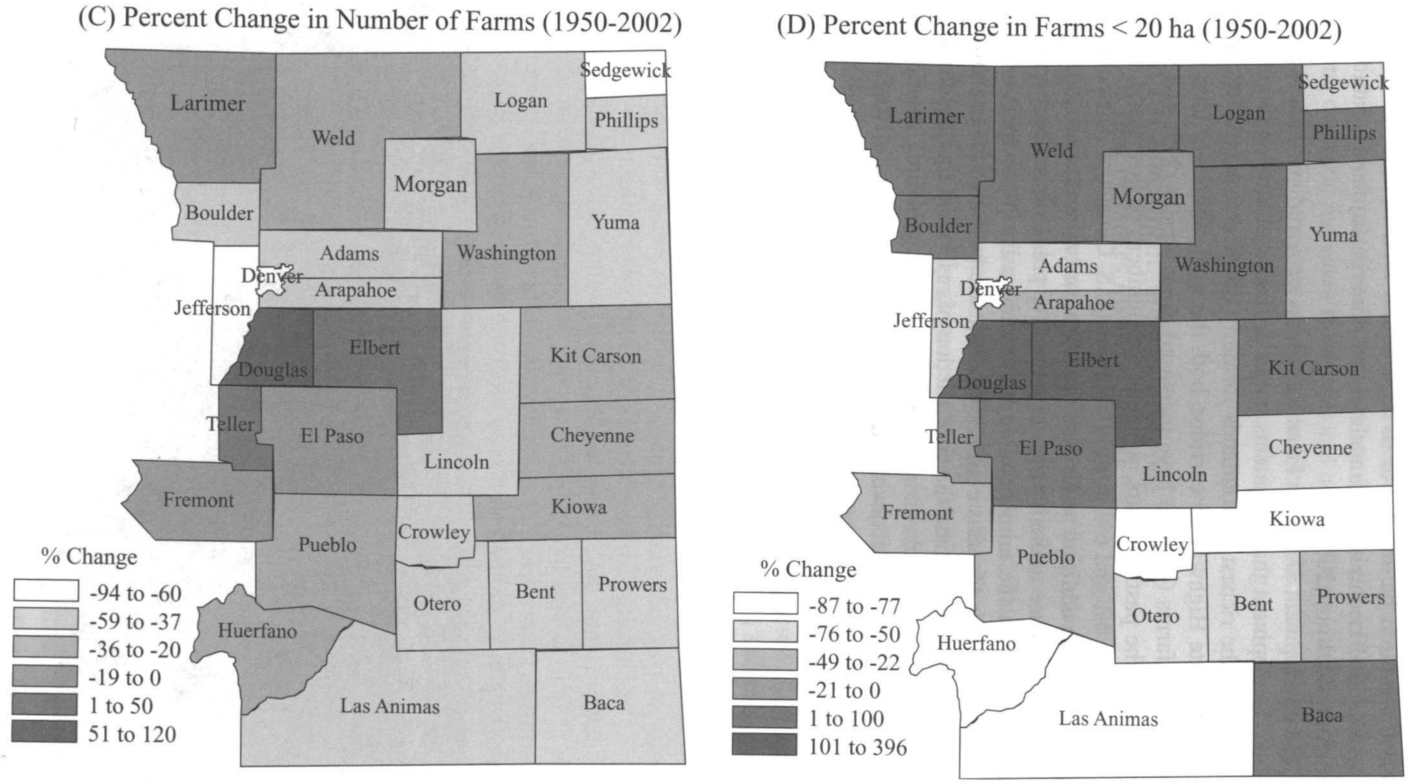

Figure 19.1 Numbers of farms (C), and numbers of farms less than 20 ha (D) since 1950 for the available census data for eastern Colorado (U.S. Census). The numbers of farms have increased because the average farm size is decreasing in the areas closest to urban growth along the Front Range of the Rockies.

Colorado Department of Local Affairs [2004]). During the same period, eastern Colorado lost 0.7 million ha, or 7%, of its agricultural land to other uses, with significant losses (10%) occurring in rangeland and other pasturelands (data from U.S. Census of Agriculture [2004]).

Much of the development along the Front Range has occurred as rural residential or exurban development that fragments larger agricultural lands into smaller parcels, particularly the richest bottomlands formerly devoted to crops. In counties along the Interstate Highway 25 corridor, both the total number of farms and the number of small farms (<20 ha) have increased dramatically (27% and 52%, respectively) during the past 20 years, whereas the numbers of farms and small farms have declined by 4% and 6% in rural counties (U.S. Census of Agriculture, 2004) (Fig. 19.1C, D). In addition to the loss of habitat, urban and exurban development leads to an increase in the number of nonnative predators such as domestic cats and dogs, and in the number of exotic and invasive plant species (Fig. 19.2) (Hanson et al., 2005; Maestas et al., 2003). Aquatic habitats also are threatened by groundwater depletion and the construction of reservoirs that accompany development, altering natural flows and turbidity, and fragmenting continuous river networks. Oil, gas, and coal development, and especially wind turbine farms (Drewitt and Langston, 2006), are emerging as possible threats to the native shortgrass steppe and wildlife in the region.

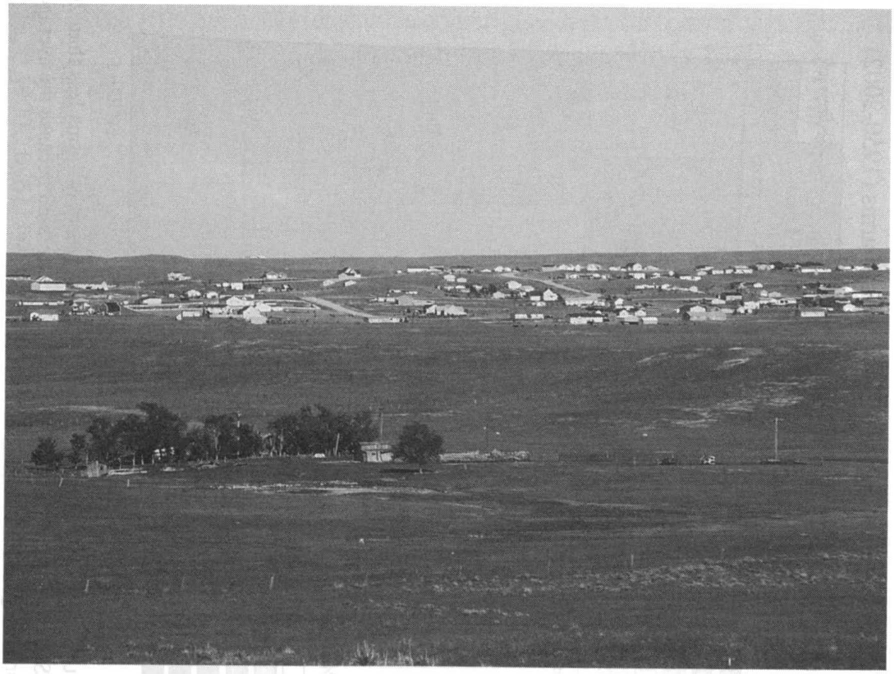

Figure 19.2 A homestead from the 1800s with current exurban growth in the background. (Photo by Justin Derner.)

On the substantial area of northern Colorado (≈80,000 ha) in public lands such as the Pawnee National Grassland (PNG), the primary land use is livestock production by local cattleman's associations. However, the PNG is currently experiencing dramatic increases in recreational use (S. Curry, personal communication, June 2006). Visitors from nearby urban areas pursue activities such as bird watching, hunting or recreational shooting, biking, hiking, and riding horses or motorized vehicles at the PNG.

Land-Use Intensification Reduces Native Species and Increases Invasive Species

Although plant and animal communities of the shortgrass steppe contain relatively few specialized or endemic species, human activities and changes in land use have led to significant declines of several native species. Thirty-eight of the 62 species of conservation concern in Colorado occur in the shortgrass steppe (Table 19.1), including three federally protected species (least tern, piping plover, black-footed ferret) and three species (black-tailed prairie dog, mountain plover, swift fox) recently petitioned for listing under the Endangered Species Act. Half of the species (18) are found in and/or near aquatic or wetland habitats, including eight species of fish and five amphibians. A number of grassland songbirds found in taller grass and shrub habitats (cassin's sparrow, brewer's sparrow, lark sparrow, grasshopper sparrow, lark bunting, western meadowlark) have suffered alarming population declines regionwide during the past three decades ($2.2 \pm 1.9\%$ decline per year [data from Rocky Mountain Bird Observatory; Colorado Division of Wildlife, 2003a]), whereas other species at risk, such as mountain plovers and long-billed curlews, are positively associated with heavily grazed grasslands.

Current wildlife conservation efforts (e.g., Colorado Division of Wildlife, 2003b) have emphasized the important ecological role of prairie dogs as prey for raptors and mammalian carnivores, and as ecosystem engineers that keep grasslands short and create burrows used by a number of other species (Kotliar et al., 1999; Stapp, 1998). Five species in Table 19.1 are closely associated with prairie dog colonies, which have declined during the past century as a result of habitat modification, widespread eradication programs, and the introduction of plague (as discussed later) (Antolin et al., 2002). In 2000, the U.S. Fish and Wildlife Service (2000) ruled that the black-tailed prairie dog warranted threatened status, but postponed formal action, citing higher priority threats to other species.

Although the petition was ultimately denied in 2004, as part of the assessment required by the petition process, states with prairie dog populations developed a multistate conservation plan (Luce, 2003), which led to a more complete inventory of the status of the black-tailed prairie dog throughout its range. An aerial survey conducted in the eastern plains of Colorado in 2001 found at least 255,000 ha of prairie dog colonies (White et al., 2005), which was 14 times more than the estimate of 17,806 ha with colonies used in the listing petition. This more accurate estimate exceeded the state's conservation target set out in the multistate plan (Luce, 2003).

Table 19.1 Species of Conservation Concern in the Shortgrass Steppe on the Eastern Plains of Colorado

Group	Conservation Status[a]	Species of Concern on Plains, %
Fishes[w]		35 (8/23)
Plains minnow	SE	
Suckermouth minnow	SE	
Brassy minnow	ST	
Arkansas darter	ST	
Plains orangethroat darter	SC	
Iowa darter	SC	
Stonecat	SC	
Flathead chub	SC	
Amphibians		
Northern cricket frog[w]	SC	86 (6/7)
Great Plains narrowmouth toad[w]	SC	
Northern leopard frog[w]	SC	
Wood frog[w]	SC	
Plains leopard frog[w]	SC	
Couch's spadefoot toad	SC	
Reptiles		
Yellow mud turtle[w]	SC	80 (8/10)
Triploid checkered whiptail	SC	
Texas horned lizard	SC	
Roundtail horned lizard	SC	
Common kingsnake	SC	
Texas blind snake	SC	
Massasauga	SC	
Common garter snake	SC	
Birds		
Least Tern[w]	FE,SE	53 (10/19)
Piping Plover[w]	FT,ST	
Western Snowy Plover[w]	SC	
Mountain Plover[p]	SC	
Long-billed Curlew[w,p]	SC	
Plains Sharp-tailed Grouse	SE	
Columbian Sharp-tailed Grouse	SC	
Lesser Prairie-Chicken	ST	
Burrowing Owl[p]	ST	
Ferruginous Hawk[p]	SC	
Mammals		
Black-footed ferret[p]	FE,SE	31 (4/13)
Black-tailed prairie dog[p]	SC	
Northern pocket gopher	SC	
Swift fox	SC	

[a]Conservation status: FE = federal endangered; FT = federal threatened; FC = federal candidate; SE = state endangered; ST = state threatened; Sc = state species of special concern.
Species denoted with a "w" are associated with aquatic systems, wetlands, riparian vegetation, or playa lakes and beaches. Associates of shortgrass steppe prairie dog colonies are denoted by a "p."
(From Colorado Division of Wildlife [2003a].)

Accurate assessments of the prairie dog abundance before European settlement do not exist. Vermiere et al. (2004) suggested that as the result of cattle grazing, by the early 20th century, prairie dog populations may have increased significantly over presettlement levels. Clearly, prairie dogs and associated wildlife on the shortgrass steppe represent an interesting case study with regard to species of concern, with little population data extending back farther than a hundred years, as well as changing scientific understanding and public perceptions.

Partly as a result of passage of the Environmental Protection Act, a ban on poisoning of prairie dogs on the PNG has been in effect since the 1970s. Shortly after the petitions for listing were filed in 1998, prairie dogs were protected from recreational shooting, and, at approximately the same time, outbreaks of plague became less extensive, possibly as a result of persistent drought. From 1998 to 2004, the total area and number of prairie dog towns increased exponentially on both the CPER (Derner et al., 2006) and the PNG (Fig. 19.3). Although after 2004, plague epizootics killed several of the largest towns, the total number of towns has continued to increase, as new towns become established and previously inactive ones are recolonized (Fig. 19.3). As of 2007, shooting of prairie dogs in Colorado was restricted only during the breeding season, from March 1 to June 14. How future changes in land use, recreational shooting, and plague will influence population fluctuations in prairie dogs and associated species remains to be seen.

Although intensified land use resulted in declines in native habitat and animal species, another important change in the shortgrass steppe has been the introduction of exotic plant species (Rickets et al., 1999). Disturbances associated with

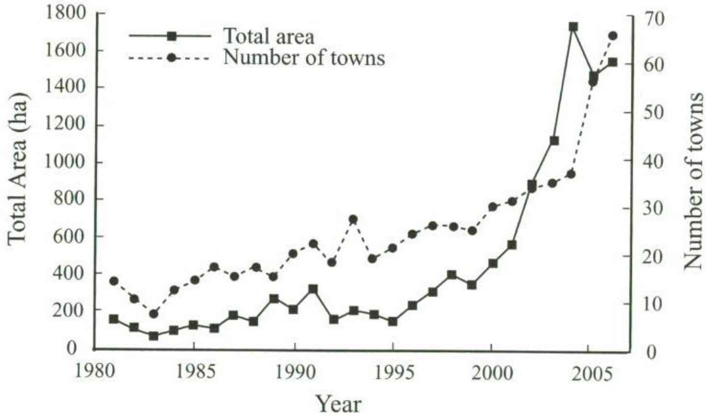

Figure 19.3 Extent of active black-tailed prairie dog towns on federally owned land on the CPER and PNG, Colorado, between 1981 and 2006. Despite outbreaks of plague that reduce total active area and lead to increases in the number of small towns (Stapp et al., 2004), prairie dogs have expanded dramatically, and currently cover between 1.5 to 2% of the 87,000-ha area. (Data from the PNG are courtesy of the U.S. Forest Service, with special thanks to Mark Ball and Elizabeth Humphrey.)

cropping (tillage, irrigation, fertilization) and residential development (tillage, irrigation, fertilization, but also pavement, road construction, and horticulture) increase the spread of plant propagules, both intentionally and unintentionally. For the shortgrass steppe, however, these disturbances function to increase the probability of survival and spread of these exotic plants, which are already part of the regional flora (Barkley et al., 1986). An important characteristic of the shortgrass steppe is that exotic plants fail to expand into uplands. The prevailing explanation for this is that native grasses—under the normal shortgrass steppe conditions of water and nutrient limitation and livestock grazing—have a competitive advantage over the exotics (Betz, 2001; Milchunas et al., 1992). However, roadsides, cropland without weed control, and abandoned croplands provide substantial opportunities for expansion of exotic plant species. Subdivision of private lands into smaller ranchettes or horse properties is very likely to increase the regional dominance of invasive and weedy species.

Land-Use Intensification Reduces Ecosystem Services

What about the effects of intensified human land use on ecosystem services such as carbon storage, the capture or production of greenhouse gases, and regional energy and water cycling? Clearly, both irrigated row–crop agriculture and urbanization increase net primary production (NPP) above that of the native shortgrass steppe. For instance, Kaye et al. (2005) estimated that within the developed area of Larimer County, Colorado, urban lawns accounted for up to 30% of the regional aboveground net primary production (ANPP) and 24% of regional soil respiration, although they occupy only 6.4 % of the area. Aboveground NPP, and hence food production, may be enhanced per unit area on irrigated cropland over native steppe, but energy-intensive additions of fertilizer, herbicides, and pesticides, coupled with transportation costs, are likely to reduce or potentially reverse net carbon capture and could lead to net carbon export at the regional scale. Carbon cycling is clearly accelerated by these land-use practices, but the regional effects on net ecosystem production or net carbon storage are unknown for the shortgrass steppe

Methane and nitrous oxide, two other important greenhouse gases with considerably stronger greenhouse effects than CO_2, are also naturally produced and consumed. Bacteria in native shortgrass steppe represent a considerable sink for methane (Mosier et al., chapter 14, this volume), but rates of methane uptake in irrigated crops and urban lawns are less than half that of the native steppe (Kaye et al., 2004; Mosier et al., chapter 14, this volume). In addition, urban lawns and irrigated crops produce 10 times more nitrous oxide than the native steppe, compounding their contribution to higher levels of greenhouse gases in the atmosphere.

Lastly, recent analyses demonstrate a significant effect of irrigated land and urban development on regional energy balance (Pielke et al., 1997), with feedbacks to precipitation. Recent atmosphere–biosphere simulation analyses (Stohlgren et al., 1998) suggest that irrigation in the Plains has resulted in decreases in July temperatures and increased stream flows in the adjacent Rocky Mountains. Despite these dynamics in which irrigation influences the Front Range, very dry years in the shortgrass steppe still occur.

Livestock Grazing Is a Management Tool in the Shortgrass Steppe

Much of the shortgrass steppe remains as native grassland because the climate is too dry to support extensive farming without irrigation. Livestock grazing continues to be the primary land use in the region and, when managed correctly, is viewed by many as compatible with multiple conservation goals (Knopf and Rupert, 1996; Maestas et al., 2003). Overgrazing may be a problem locally, especially in sensitive riparian areas (Fleischner, 1994), but the relatively low productivity of the shortgrass steppe makes widespread overgrazing economically unsustainable. In much of the western United States, one of the most economically and ecologically significant changes in rangeland ecosystems is the arrival and spread of invasive plants. Exotic plants can reduce forage quantity and quality, alter ecosystem function, and reduce biological diversity (DiTomaso, 2000; Masters and Sheley, 2001). As mentioned earlier, the native shortgrass steppe is highly resistant to exotic plant invasion, and cattle grazing intensity is inversely related to exotic species richness (Milchunas et al., 1990, 1992). Thus, domestic livestock may be an effective means of controlling the spread of some exotic plants.

It is likely that traditional ranching with uniform grazing has resulted in a less heterogeneous grassland than existed before European settlement, in part because of changes to natural disturbance regimes (including fire), and in part to changes in grazing patterns caused by the fencing in of open range and the switch from native to domesticated grazers. Recently, Fuhlendorf and Engle (2001) proposed that grazing management should "enhance heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock." page 625. They advocated management approaches that simultaneously address the objectives of conservation biologists, ecologists, and rangeland managers. Contemporary approaches to grazing management incorporate the view that herbivores and the rangeland manager are both components of a complex ecosystem (Whalley, 2000) that requires multiple-use management to accommodate a diverse array of products and services.

Implicit is the notion that grazing management influences both the structure and function of rangeland ecosystems, and also influences ecosystem services. Rangeland managers have attempted to accommodate this by using cattle to manipulate species composition (Milchunas and Lauenroth, 1993), plant community structure (Milchunas and Lauenroth, 1989; Sala et al., 1986), and spatial heterogeneity of vegetation (Adler et al., 2001). Ecosystem services include maintenance or enhancement of biological diversity, carbon sequestration, increased water quality, and reduction of invasive weeds. Collectively, contemporary approaches to grazing management address the need for more sustainable rangelands while satisfying the public's recreational and aesthetic desires. As Briske (1993) stated "the sustainability of grazed systems is a more fundamental issue than grazing optimization." page 24.

However, current ecosystem-oriented approaches to grazing management alone are not able to achieve all conservation goals, being somewhat limited in the ability to create or modify habitats to the extent required for specific wildlife species of concern. In some cases, private land managers may be willing to modify management practices to produce species-specific habitat modifications, especially if financial support through direct payments or economic incentives is available. For example, seasonal or short-term intensive grazing may be used to create mosaics of habitat for species of grassland birds such as mountain plovers, which require extremely short vegetation for nesting and chick rearing (Knopf and Miller, 1994). In other cases, such as in riparian areas, the ecological costs of livestock grazing may prohibit its use as a management tool (Fleischner, 1994).

Conservation goals often vary between groups of users of the shortgrass steppe. At times, discord can arise between these groups in trying to develop a single management procedure to achieve diverse and sometimes divergent products and outcomes. One particular challenge is to devise approaches that meet the recreational needs of the public. On the shortgrass steppe, using grazing as a primary management tool has the advantage of being compatible with ecosystem and species-level approaches to conservation, with the socioeconomic status of rural communities, and with the ranching way of life (Knight et al., 2002).

Conservation Strategies

> *A prairie like that, one big enough to carry the eye clear to the sinking, rounding horizon, can be as lonely and grand and simple in its forms as the sea. It is as good a place as any for the wilderness experience to happen; the vanishing prairie is as worth preserving for the wilderness idea as the alpine forest.*
>
> —Wallace Stegner (1969, p. 152.)

Although rapid population growth along the eastern edge of the Rocky Mountains poses a great threat to the native shortgrass steppe, large tracts of it persist. Many of these tracts are on private lands, but many others are in public landholdings. To be effective, conservation approaches require the cooperation of many diverse entities, including private landholders, public agencies, land trusts, conservancies, and environmental groups. Increasing concerns about loss of rural cultures, populations, and agricultural/rural landscapes have led to conservation assessments that focus on ecosystem services (Theobald, 2003), and in some cases, economic incentives such as conservation easements (Kabii and Horwitz, 2006; Newburn et al., 2005). Conservation easements are an increasingly important land use that will shape the landscape into the future.

We expect that future conservation strategies with the greatest chances of success will do the following:

1. Advocate ecosystem-level conservation based on sound science, taking into account that agriculture-based economies provide the best hope for conserving large tracts of open space in the region (Knight et al., 2002). For the most part, this will consist of livestock production, because the shortgrass steppe is extremely slow to recover from tilling that disrupts the soil. In abandoned croplands, landowners should be encouraged to plant native species, including local genetic stocks, for revegetation and soil recovery efforts.

2. Promote grazing practices that restore structural and compositional heterogeneity to grasslands on a landscape scale, while minimizing detrimental effects on the most ecologically sensitive areas (e.g., riparian areas). Ideally, management at small scales (i.e., pastures, allotments) would collectively enhance heterogeneity at larger scales (i.e., watersheds, landscapes), such that the desired outcome would consist of a mosaic of natural habitats with differing serial stages of vegetation comprising an array of heights and types of plants that enhance ecosystem services (e.g., biodiversity) and amenities (recreation, wildlife viewing) for the public. Restoration of natural grazers such as bison and prairie dogs in large remaining tracts of grassland is one approach to meeting these goals that will enhance the conservation value of these lands, particularly with respect to restoring native dominant organisms.
3. Provide incentives to ranchers and farmers to maintain their land as functional open space, and target areas where large, contiguous areas of grasslands can be protected from development. Effective conservation of the shortgrass steppe will require protection of the most ecologically valuable and threatened tracts. Although some of the recent conservation efforts have focused on the important ecological role that prairie dogs play in the shortgrass steppe, we should recognize that some tracts of land may include areas not capable of supporting colonies of prairie dogs. Conservation easements between private landholders and local land trusts and national organizations allow for the purchase or protection of lands and development rights. Federal programs developed under the Farm Bill, such as the Farm and Ranch Lands Protection Program, Grasslands Reserve Program, provide funds and support for these agreements.

Urban open spaces, even areas that retain shortgrass plant communities or prairie dogs, may be population sinks or ecological traps (Battin, 2004; Kristan, 2003) for many species. Although these areas have recreational, educational, or aesthetic utility, they may be of minimal ecological value for plant and animal communities, or for other ecosystem services, because of their small size and isolation. However, they provide recreation for some, and are very important educational opportunities for urban residents to learn about the values and characteristics of grasslands.

Implications of Global Change

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Rates of Global Change

Today, scientists broadly agree that greenhouse gases like CO_2, nitrous oxide, and methane will continue to increase in the earth's atmosphere, although there is still debate about the rate at which these gas emissions are increasing, and the consequences for climate change around the world. Releases of significant quantities of CO_2, nitrous oxide, and methane into the atmosphere began during the Industrial Age, and continue today at increasingly higher rates (Parry et al., 2007). Anthropogenically driven global warming was detected during the 20th century, and is expected to increase significantly during the 21st century. Predicted changes in precipitation dynamics are complex and variable among world regions, but are expected to lead to more intense storms, which will increase surface runoff and erosion in some regions (Campbell et al., 1997). Nitrogen availability is increasing globally (Vitousek et al., 1997), particularly in grassland regions, as a result of high rates of fertilization coupled with urbanization (Burke et al., 2002). With few exceptions, the potential interactions of these and other less studied global change factors (ultraviolet radiation, ozone) have yet to be evaluated in multifactor experiments, nor have management practices been considered in the context of most global change experiments. So although global change is an agreed-upon certainty, its extent and impact are still unknown. The effects of global change are likely to be experienced in virtually all world ecosystems, including the shortgrass steppe, where we expect sensitivity to be high.

Water and Temperature Will Continue to Be Important

There are good reasons to suspect that the shortgrass steppe may be sensitive to several features of global change. Like most terrestrial ecosystems, spatial and temporal variations in temperature and precipitation affect the geographic extent of the shortgrass steppe (Lauenroth and Milchunas, 1991; Stephenson, 1990), the balance and productivity of species within its different regions (Alward et al., 1998; Coffin and Lauenroth, 1996; Epstein et al., 1997, 2002; VEMAP Members, 1995; Lauenroth et al., chapter 17, this volume), the structure of the plant community (Alward et al., 1998; Milchunas et al., 1989; Lauenroth, chapter 5, this volume), and the cycling of key nutrients (Burke et al., 1997a,b; Burke et al., chapter 13, this volume) and water availability (Lauenroth and Bradford, 2006; Lauenroth and Milchunas, 1991). Water is a key environmental driving variable in this semiarid grassland, with variations in annual amount and distribution causing large changes in ANPP (Lauenroth and Sala, 1992; Milchunas et al. 1994), and ultimately resulting in plant community shifts (Milchunas and Lauenroth, 1995). Thus, any fluctuations in water status, whether driven directly by altered precipitation patterns or indirectly through increased evapotranspiration under warmer temperatures, are certain to have impacts on the ecology, land use, and overall economics of this grazing land. Increases in temperature will alter the boundaries and species composition of the shortgrass steppe, and may increase productivity with extension of the growing season, provided temperature increases are not so severe that the desiccation response prevails.

Carbon and nitrogen cycling, and carbon storage are also sensitive to changes in precipitation and temperature (Burke et al., 1997a; Epstein et al., 2002; Lauenroth et al., 2004). Simulation results (Parton et al., chapter 15, this volume) suggest that total ecosystem carbon will decrease under all scenarios that include an increase in temperature, because of the sensitivity of decomposition to increased temperature. Increases in precipitation alone would likely result in increases in all fluxes, including NPP, respiration, and greenhouse gas fluxes to the atmosphere. In these simulations, the only climatic change that results in increased carbon storage is addition of nitrogen; all other changes result in either no change or losses of total carbon and nitrogen. Current long-term studies on the CPER support these simulations with respect to warming, wetting, and drying.

There are strong interrelations between climate and land-use management in the shortgrass steppe (Lauenroth et al., chapter 1, this volume). After grazing, the second most important land management type on the shortgrass steppe is dryland winter wheat (Lauenroth et al., 1999, 2000), managed with a fallow rotation. The western edge of the shortgrass steppe lies at the margin of viability for dryland wheat, and any decreases in precipitation or increases in evapotranspiration rates (both are likely with increasing temperature) may reduce the feasibility of growing wheat. Although wheat is the dominant crop by area, irrigated crops are by far the largest source of revenue; these crops are dependent upon a reliable source of surface or groundwater. Decreases in precipitation, combined with competition from urban subdivisions for water, could decrease the amount of irrigated cropland on the shortgrass steppe.

Responses to Carbon Dioxide Are Important as Well

Increases in atmospheric CO_2 are likely to have a greater impact on the shortgrass steppe than on many other ecosystems, largely because of water relations and the sensitivity of this region to water. Although increases in atmospheric CO_2 have been studied mostly in terms of the effects of enhanced photosynthesis on ecosystem functioning, the indirect effects on soil–plant water relations can be important as well. Increasing ambient CO_2 levels induces stomatal closure in most herbaceous species (Kimball and Idso, 1983; Morrison and Gifford, 1983; Wand et al., 1999), resulting in altered seasonal water dynamics and increased plant water use efficiency (Morgan et al., 2004b). This water relations response to elevated CO_2 may account in large part for the strong and consistent production increases to elevated CO_2 in the shortgrass steppe (LeCain et al., 2003; Milchunas et al., 2004; Morgan et al., 2001, 2004b; Nelson et al., 2004). Water-driven responses appear to be the dominant mechanism behind CO_2-induced production increases in semiarid systems and during dry spells in more mesic, native (or seminative) grasslands (Morgan et al., 2004b; Niklaus et al., 1998; Owensby et al., 1996b). Collectively, these findings suggest that global change will primarily affect systems like the shortgrass steppe through the indirect effects on water relations and interactions with temperature.

Nutrient Cycles Will Be Altered by Increased Carbon Dioxide, but Slowly

One of the more consistent responses to elevated CO_2, especially in systems exhibiting relatively large increases in NPP, is a decline in shoot nitrogen concentration (King et al., 2004; Milchunas et al., 2005; Morgan et al., 2004a). Although lower tissue nitrogen concentration may be partially attributed to the higher nutrient use efficiency that plants experience at elevated CO_2 (Drake et al., 1997), the accumulation of nitrogen in organic compounds at elevated CO_2, and the inability of the soil to release nitrogen quickly enough to meet the increased growth are more likely to be important on the shortgrass steppe (Luo et al., 2004; Reich et al. 2006a,b; Zak et al., 2000). Low-productivity ecosystems such as the shortgrass steppe are characterized by slow decomposition and nutrient mineralization, and low rates of nutrient supply (Burke et al., 1997a; Epstein et al., 2002; Wardle et al., 2004), and may be particularly vulnerable to the feedback of CO_2 on soil nitrogen supply. This low level of soil biological activity may account for the lack of significant effects of elevated CO_2 on fluxes of CO_2, methane, $NO_{x,}$ and nitrous oxide during the course of a 5-year CO_2 enrichment experiment at the CPER (Mosier et al., 2002), despite significant effects on plant production (Milchunas et al., 2004; Morgan et al., 2001, 2004a). Slow nutrient cycling in such systems may also increase the time required for responses to perturbations such as increased CO_2 or altered temperature. This means that results from relatively short-term studies (<10 years) will not necessarily suffice for predicting the effects of incremental global change during the next hundred years (Morgan, 2002; Zak et al., 2000).

Species Responses to Carbon Dioxide Matter, But Are Difficult to Predict

Results from experiments conducted in the shortgrass steppe provide some insight into how individual species and functional groups will respond to increasing atmospheric CO_2 (Morgan et al., 2004b, 2007; Nowak et al., 2004). Increases in productivity and cover have tended to be more pronounced for C_3 than C_4 grasses (Morgan et al. 2004a; 2007), as predicted by differences in photosynthetic pathways (Polley, 1997). However, the response of C_3 grasses is not via photosynthesis, but by greater seedling recruitment of the C_3 perennial grass *Stipa comata*. Furthermore, photosynthesis, water relations, and productivity of dominant shortgrass steppe grass species, C_3 and C_4 alike, can respond to CO_2 (Hunt et al., 1998; LeCain et al., 2003; Morgan et al., 1994). Species shifts in the shortgrass steppe caused by increasing CO_2 will ultimately depend on complex interactions among the plant community, the soils, and the climate (Morgan et al., 2004a), and will not be easily predicted by differences in a single attribute like the photosynthetic pathway. Incorporating multiple plant mechanisms into models that accurately predict species responses to CO_2 and other environmental variables will be a challenge.

An example of surprising responses is the 40-fold increase in aboveground biomass of the C_3 subshrub *Artemisia frigida* during 5 years of CO_2 enrichment, which involved the interaction of several plant mechanisms and a drought (Morgan et al., 2007). Basic information on how critical plant species acquire and use water to produce biomass, participate in soil–plant nutrient cycling (King et al., 2004; Mosier et al., 2003), and recruit new individuals (e.g., Peters et al., chapters 6 and 7, this volume) must be integrated into models to predict confidently how productivity and plant species composition in the shortgrass steppe will shift in the face of increasing atmospheric CO_2.

Ultraviolet Radiation Is an Important Current Control and Its Importance May Increase in the Future

Another aspect of climate change is the potential for alterations in levels of ultraviolet radiation reaching the earth's surface, which may increase because of depletion of ozone, or may decrease if cloudiness or particulates in the atmosphere increase. Ultraviolet radiation affects decomposition rates in the shortgrass steppe and similar dry areas of the world (Austin and Vivanco, 2006; Parton et al., 2007b). A short-term study of ultraviolet effects on plant production and decomposition at the shortgrass steppe suggests complex interactions with elevated atmospheric CO_2. In contrast to increases in production with elevated CO_2, ultraviolet radiation decreased primary production (Milchunas et al., 2004). These interactions among various aspects of climate change and different species responses to CO_2, temperature, and ultraviolet radiation highlight the challenges associated with predicting the effects of global change.

Future Directions in Climate Change Research and Implications for Management

Our experience in the shortgrass steppe indicates that global change is likely to have important effects primarily through its impact on water relations, but that feedbacks involving nutrient cycles may be important as well. Primary production is responsive to CO_2, and nitrogen-releasing reactions appear unable—in the short term—to meet the higher nitrogen demand completely when CO_2 increases. Thus, the carbon-to-nitrogen ratio of the system may increase, with repercussions for plant nutrient status, soil biology, and whole-system nitrogen cycling (Luo et al., 2004; Reich et al., 2006b; Zak et al., 2000). An important economic consequence may be a reduction in forage quality below levels for sustainable livestock production (Milchunas et al., 2005). This response has been observed in other grasslands (Körner, 2000; Owensby et al., 1996a), and seems to be one of the more predictable responses in grasslands that experience significant production responses to CO_2. Changes in species composition such as those that occurred in the CO_2 enhancement experiment (Morgan et al., 2004a) may contribute to a decline in forage quality, although our ability to extrapolate this response to other regions of the shortgrass steppe is uncertain because of the variability of species composition in plant communities (Lauenroth and Milchunas, 1991).

As we design future global change experiments, considerable care should be taken in selecting which factors to impose in multifactor field experiments, and which ones we must be content to model. Considerations for selection criteria include current knowledge gaps, cost, ability to impose realistic treatments, ability to extrapolate and model results, and potential uses of research for management and policy.

Ecological Consequences of a Changing Disease Environment

Michael F. Antolin

Changing land use on the grassland, combined with increases in CO_2, climate change, and invasions by exotics, will also create new opportunities for pathogens to spread, with as-yet unknown ecological consequences. It is increasingly apparent that local prevalence and outbreaks of infectious diseases can be influenced by large-scale climatic patterns like those driven by El Niño Southern Ocillation (ENSO), the periodic surface warming of the southern Pacific (Anderson et al., 2004; Harvell et al., 2002; Pascual and Dobson, 2005; Stapp et al., 2004). In most cases, the mechanisms associated with ENSO-driven disease cycles are unknown, but it is hypothesized that changes in temperature and precipitation trigger cascades that increase or decrease primary productivity. In turn, changing resources alter host density and contact rates between hosts and/or the insect vectors that transmit the pathogens (Dobson and Foufopoulos, 2001; Gratz, 1999; Jones et al., 1998; Parmenter et al., 1999). Perturbations within ecological communities lead to changing epidemiological conditions and rates of disease transmission, with either amplification of pathogens to epidemic levels, or declines back to low-level persistence. Within these broad patterns, however, the mechanisms that permit both disease outbreaks and low-level persistence remain to be explored (Harvell et al., 2002).

The changing disease environment on the shortgrass steppe may have three direct ecological consequences: (1) change in fauna and flora mortality caused by exotic pathogens, and resulting changes in community structure; (2) altered frequency of disease outbreaks triggered by climate cycling between droughts and cooler periods with more abundant rainfall; and (3) greater exposure of humans and their domestic animals to pathogens when they move to exurban homes surrounded by the grasslands. A fourth possibility—that native pathogens of both plants and animals increase in frequency—will be considered at the end of this section.

We can illustrate the effects of a changed disease environment by the best-studied disease system on the shortgrass steppe: the black-tailed prairie dogs and sylvatic plague (the name given to the disease when it cycles in wild populations). The case of the black-tailed prairie dog illustrates how single species may be affected, but also shows that in many instances the changes could be communitywide, especially if the pathogen infects keystone species like prairie dogs (Antolin et al., 2002; Kotliar et al., 1999; Stapp, 1998). Besides, we may expect a continued stream of new introductions of both plant and animal pathogens, much as we see an onslaught of introduced weedy plants and animals (Anderson et al., 2004; Dobson and Foufopoulos, 2001). Recently introduced animal pathogens include West Nile virus, which found a good home in the western United States, where an effective mosquito vector (*Culex taraslis*) already resides, and the monkeypox virus, which was introduced into the United States via the exotic pet trade from Africa, but apparently failed to establish. Furthermore, climate change may play a role in the severity of pathogen introductions. For instance, plant fungal and bacterial pathogens show greater rates of introduction and emergence with climate change (especially increased moisture), whereas plant viruses seem to be unaffected by climate (Anderson et al., 2004).

Plague, caused by the bacterium *Yersinia pestis*, is primarily a disease of rodents spread by fleas, although it is best known for the high mortality it caused historically during human epidemics (Poland and Dennis, 1998). The eastern extent of plague in wild rodents is near the 97th meridian in southern Texas, extending northward to the 102nd meridian in North Dakota (Antolin et al., 2002; Barnes, 1993). In the absence of significant climate change, plague is not expected to spread farther eastward, because previous introductions into ports along the Atlantic and Gulf coasts of the United States failed to establish sylvatic plague in the eastern part of the United States. Worldwide plague foci persist in semiarid ecosystems with populations of burrowing rodents, including the western United States (Poland and Dennis, 1998).

The first large-scale die-offs of prairie dogs in northeastern Colorado were reported in 1948 (Ecke and Johnson, 1952), and plague has recurred here since that time (Centers for Disease Control and Prevention, unpublished records). Outbreaks of plague decimate local populations of prairie dogs, with mortality usually reaching 100% (Barnes, 1993). Long-term monitoring (1981 to present; Fig. 19.3) on the PNG revealed that prairie dogs persist as a metapopulation, with local extinctions followed by recolonization 2 to 4 years later (Roach et al., 2001; Stapp et al., 2004, chapter 8, this volume). By changing the population dynamics of prairie dogs, plague has had devastating effects on the black-footed ferret, possibly the most endangered mammal in North America. Abundance of three bird species (burrowing owl, ferruginous hawk, and mountain plover) also tends to fluctuate along with prairie dog populations (Antolin et al., 2002).

The effects of climate on incidence of plague were first noted in northern New Mexico and Arizona, where rainfall, summer temperature, and habitat characteristics (e.g., piñon pine and juniper) all influence transmission of plague from rodents to fleas to humans (Enscore et al., 2002; Parmenter et al., 1999). Our own studies (Stapp et al., 2004) suggest a similar link between prairie dog die-offs and cooler/moister summers on the shortgrass steppe during ENSO years. It remains to be seen whether the climate affects the pathogen directly, alters the reproduction of flea vectors, or changes dynamics of the entire rodent community (Gage and Kosoy, 2005).

How will the disease environment change in the future? We have already considered some effects of exotic pathogens like plague, but this question brings up the fourth disease possibility: strong emergence of native pathogens that currently exist at low levels. Disease emergence may have two sources: direct environmental changes by humans, and emergence as a consequence of climate change. A clear example of human impacts is the emergence of the bacterial pathogen that causes rabbit fever (tularemia) in prairie dogs that were captured and held in captivity for the exotic pet trade (Avashia et al., 2004). Similarly, domestic animals can transmit disease to wild populations: The last black-footed ferrets in Wyoming were taken into captivity to avoid an outbreak of canine distemper virus. With larger populations of both humans and their domesticated plants and animals, the risk of pathogen transmission from wild to domesticated populations is bound to increase, and vice versa (Weiss and McMichael, 2004). The effects of climate change are more complex, because some conditions favor pathogen spread while others slow it (Harvell et al., 2002). For instance, drought could reduce disease risk in plant species, because pathogenic fungi and bacteria require relatively moist conditions for transmission. On the other hand, drought could increase spread of animal pathogens if animals aggregate around scarce resources (e.g., water) during droughts. Great consideration also must be given to changes in geographic distribution in relation to climate change. Pathogens that are common in warmer southern regions of North America may spread northward as temperatures increase, especially if their most common hosts also shift their ranges northward.

In sum, changes in the disease environment on the shortgrass steppe parallel closely the changes expected after the introduction of exotic animals and plants, the effects of human disturbances on plant and animal communities, and the influence that climate change will have on the range and abundance of potential host species. The greatest ecological effects will be seen in alteration of keystone species like prairie dogs, or dominant species like blue grama and buffalograss. Regardless, the possibilities warrant continued vigilance and surveillance.

Conclusion

Ingrid C. Burke and William K. Lauenroth

Long-term research in the shortgrass steppe has taught us one very important lesson: The steppe changes slowly in response to environmental changes that fall within its evolutionary and developmental history, a history that has included drought and herbivory. Because of the character of these two forces, much of the richness of the shortgrass steppe exists belowground. The most rapid changes in the absence of humans occurred during and after the Pleistocene, and were associated with arid times that produced high rates of erosion and deposition (Kelly et al., chapter 3, this volume). However, even these changes took place over thousands of years, and we now think that soil instability occurred because *B. gracilis* was not present. The dominant organisms and structure of the native steppe have been relatively constant since then, even in the face of extended drought.

Now and into the foreseeable future, the shortgrass steppe is facing unprecedented changes wrought by humans: land-use change, global change, and changes in diseases. How will the shortgrass steppe respond? Except in the most dramatic of changes (exurbanization, cultivation management, combined with drought and wind), we are confident of three things: (1) the native portions of the shortgrass steppe will respond slowly; (2) many of the changes will be hidden from view, occurring below the soil surface, where by far the largest proportion of biological activity occurs; and (3) long-term sustainability will be determined by the landscape to regional-scale context of the changes. Continued research over long periods, including research that applies the newest techniques, that increases our understanding belowground, and that allows us to scale to the regional view, will give us the largest likelihood of predicting the future.

The sun burns the snow high on the mountains
It runs and it grows as it falls
Silt and soil
Down it boils
Down to the valleys,
The gold river rolls to the plains

The rangeland lies high, up from the river
The coolies are dry where the shortgrass grows
Fields of hay, cottonwood shade
Green patch of home through the high dusty land
The river flows

Early evening light, boys practice roping
The day fades away, the night rolls on.....
Lives of pride
Men who ride
They keep the old skills that came up the trail from Mexico

The long river winds through green years and dry years
Brand 'em in the spring, ship 'em in the fall
The new colt foaled, the mare grows old
Cycle of changes in this changeless land where the shortgrass grows
In this changeless land where the shortgrass grows

Ian and Sylvia Tyson, "The Short Grass"

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